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Biological traits and life table of the exotic *Harmonia axyridis* compared with *Hippodamia variegata*, and *Adalia bipunctata* (Col., Coccinellidae)

A. Lanzoni, G. Accinelli, G. G. Bazzocchi and G. Burgio
Dipartimento di Scienze e Tecnologie Agroambientali-Entomologia, Alma Mater Studiorum-Università di Bologna, Bologna, Italy

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Abstract: As part of an environmental risk assessment study of exotic natural enemies used in inundative biological control, life-history characteristics of *Harmonia axyridis* (Pallas), *Hippodamia variegata* (Goeze) and *Adalia bipunctata* (L.) (Col., Coccinellidae) were quantified under laboratory conditions at 25°C on *Myzus persicae* (Sulzer) as prey. Comparative studies showed significant differences among pre-adult development times: *H. axyridis* developed slower ($\bar{X} = 19.8$ days) than *H. variegata* ($\bar{X} = 18.1$ days) and *A. bipunctata* ($\bar{X} = 18.4$ days). Differences were also evident in the duration of egg, larval and pupal stages. No measurable differences among the three species were found for fecundity, oviposition rate and adult longevity. *Harmonia axyridis* exhibited the longest pre-oviposition ($\bar{X} = 7.4$ days) and interoviposition ($\bar{X} = 3.6$ days) periods and the shortest oviposition period ($\bar{X} = 13.7$ days). The Bieri model was used to describe age-specific fecundity for the three species of coccinellids. The intrinsic rate of increase (r_m), net reproductive rate (R_0) and mean generation time (T) were higher for *H. variegata* ($r_m = 0.114$, $R_0 = 52.75$, $T = 41.88$ days) than for *H. axyridis* ($r_m = 0.089$, $R_0 = 26.27$, $T = 38.81$ days) or *A. bipunctata* ($r_m = 0.081$, $R_0 = 18.49$, $T = 40.06$ days). Our findings show that the biological traits of *H. axyridis* do not seem to be factors that may contribute to the invasiveness of this coccinellid.

Key words: *Adalia bipunctata*, *Harmonia axyridis*, *Hippodamia variegata*, development time, environmental risk, fecundity, life table parameters

1 Introduction

The Asian multicoloured ladybeetle *Harmonia axyridis* (Pallas) is a Palearctic polyphagous species originating from the Far East. This arboreal ladybird occurs in orchard and forest habitats and preys mostly on various aphid species, but it also accepts scales and two species of chrysomelids (Tedders and Schaefer, 1994). Because of its good searching capacity and predation activity, *H. axyridis* is an effective biological control agent against aphid pests. It has been introduced in France by I.N.R.A. in 1982 (Ferran et al., 1996); it has also been introduced and established in the United States (LaMana and Miller, 1996; Brown and Miller, 1998; Colunga-Garcia and Gage, 1998; Brown, 1999), in Canada (Coderre et al., 1995) and released in Italy.

It is well known that the introduction of generalist entomophagous insects could cause environmental risks. In particular these problems could regard intraguild competition, with negative effects on native species (Simberloff and Stiling, 1996; Thomas and Willis, 1998).

At present, no data about negative effects of the introduction of *H. axyridis* in Europe are available. Regarding the USA, field surveys by Brown and Miller (1998) in West Virginia, revealed that by 1995 *H. axyridis* had become dominant in the Coccinelline tribe, continuing to dominate the Coccinelline guild on apple. According to these authors the exotic species *Coccinella septempunctata* (L.), that had been present in the region since 1983, had been displaced by *H. axyridis*. This species was found by Colunga-Garcia and Gage (1998) to have become a dominant coccinellid in the agricultural landscape of southwestern Michigan. Adults were reported for all the habitats sampled, including early secondary succession, poplar plantation, alfalfa, soybean, corn and winter wheat crops.

A methodology for risk assessment has been developed as a basis for regulation of import and release of exotic natural enemies (van Lenteren et al., 2003). In this contest biological traits are essential for assessing the potential rate of population increase of a species, thus providing, together with other parameters, a

theoretical evaluation of the potential of an exotic natural enemy to compete with native species.

Laboratory experiments were carried out to study the life history of the exotic species *H. axyridis* and, as a comparison, of the native species *Adalia bipunctata* (L.) and *Hippodamia variegata* (Goeze). These two indigenous species were chosen because they are common in hedgerows and orchard trees (Hodek and Honěk, 1996) and abundant in the agroecosystems of northern Italy (Boriani et al., 1998; Ferrari et al., 1998; Burgio et al., 1999). *Myzus persicae* (Sulzer) was chosen as prey because its widespread occurrence and harmfulness make it a relevant target for inundative release of coccinellids. The biological traits of the three coccinellids species, including development time, fecundity, adult longevity and life-table, were compared.

2 Materials and Methods

2.1 Insect rearing

Aphids and coccinellids were reared in the entomological laboratories of DiSTA (Dipartimento di Scienze e Tecnologie Agroambientali), University of Bologna. Cultures of *A. bipunctata* and *H. variegata* were derived from field-collected specimens; *H. axyridis* was supplied by Koppert (The Netherlands). Larvae of the three coccinellid species were fed with frozen eggs of *Ephestia kuehniella* Zeller. Adults were fed with *M. persicae* that had been reared on 'Primizia' green pea (*Pisum sativum* L.) sprouts. Adult coccinellids were maintained in Plexiglas cages ($40 \times 30 \times 45$ cm) and larvae in plastic cylinders (Kartell®, Milan, Italy) ($Ø = 18$ cm, $h = 18$ cm). Both adults and larvae were kept at 20–25°C with a relative humidity of 60–80%, L : D = 16 : 8.

2.2 Experiments for determining biological traits

Egg masses from each of the three coccinellid species were placed separately in cylindrical containers ($Ø = 9$ cm, $h = 28.5$ cm, thickness = 4 mm) that were then kept in an environmental chamber (25 ± 1°C, UR = 60–80%, L : D = 16:8). The new-hatched larvae were reared on *M. persicae* until adult eclosion. The sex of the adults was determined. Ten pairs (male and female) of *A. bipunctata* and *H. variegata* and eight of *H. axyridis* were selected. Adults were taken from different containers to avoid the inbreeding of siblings. Each pair was put in a Plexiglas cylindrical cage ($Ø = 9$ cm, $h = 28.5$ cm, thickness = 4 mm) that was covered with a screened lid. Each cage was lined on the inside with an air bubble plastic film to act as oviposition substrate. The adults were daily fed *ad libitum* with *M. persicae* infesting fresh sprouts. Dead aphids and old sprouts were removed daily. The number of eggs laid by each female, including the cannibalized ones, was recorded daily until the female's death. Any deceased males during the experimental period were replaced. The pre-oviposition period was calculated as the number of days between emergence and the first oviposition, while the interoviposition one as the number of days between two subsequent ovipositions. Finally, the oviposition period was made up of the interoviposition period plus the number of days during which oviposition occurred.

In order to determine pre-imaginal development times, pre-imaginal survival, and sex ratio of the three species, 10 eggs were collected from different females of each species, starting on the fifth day after the first oviposition. The operation was repeated every 10 days throughout female lifespan until 50 eggs were collected for each species. The eggs were incubated at 25 ± 1°C, UR = 60–80%, L : D = 16:8 and placed individually in cylindrical containers ($Ø = 4$ cm, $h = 4$ cm, thickness = 2 mm) to avoid larval cannibalism. Eggs were checked daily for hatch. Larvae were fed *ad libitum* with *M. persicae* and examined every day for ecdysis. Only the individuals reaching adulthood were taken into consideration for determining development times of each instar. After emergence adults were sexed. The experiment was replicated twice for a total of 20 pairs (15 for *H. axyridis*), development times being determined on the basis of 85 eggs for *H. axyridis* 108 eggs for *H. variegata* and 100 eggs for *A. bipunctata*.

The intrinsic rate of increase (r_m) was calculated by the Birch (1948) method, that is based on the equation of Lotka; r_m can be determined by iteratively solving the equation:

$$\int_0^n \exp(-rt) l_x m_x = 1,$$

where m_x is the age-specific fecundity and l_x is the survival (Dent, 1997). Net reproductive rate (R_0), and mean generation time (T) were calculated by the following formulas:

$$R_0 = \Sigma l_x m_x,$$

$$T = \Sigma x l_x m_x / \Sigma l_x m_x.$$

The parameters of the life-table were estimated on the basis of the sex ratio noticed in our experiments.

Voucher specimens of *A. bipunctata*, *H. variegata* and *H. axyridis* have been deposited into the Dipartimento di Scienze e Tecnologie Agroambientali insect collection, Alma Mater Studiorum-Università di Bologna.

2.3 Statistical analysis

Data on development times and on reproduction patterns were studied by analysis of variance (anova), and means were separated using Tukey's honestly significant differences (HSD) procedure ($P < 0.05$). Differences in pre-imaginal survival were analysed using χ^2 contingency tables (Zar, 1984). The relationship between female age and oviposition rate (number of eggs laid/female/day) was fitted by the Bieri model (Bieri et al., 1983):

$$y = [P_1(x - P_2)]/\{\exp[\ln(P_3)(x - P_2)]\},$$

where x = age of female (days), and P_1, P_2 and P_3 are coefficients.

The STATISTICA software for Windows StatSoft™ (1994) was used for statistical analysis.

3 Results and Discussion

There were significant differences in pre-adult development times ($F = 13.79$; d.f. = 2, 115; $P < 0.0001$) (table 1). In particular, *H. axyridis* took about 1.5 more days to complete its development than *H. variegata* and *A. bipunctata*. Overall, the larval stage was significantly longer in *H. axyridis* than in the other two species ($F = 8.19$; d.f. = 2, 115; $P = 0.0005$), and some significant differences were found among the three species in the first ($F = 5.90$; d.f. = 2, 115; $P = 0.0036$), second ($F = 6.48$; d.f. = 2, 115; $P = 0.0022$) and fourth ($F = 55.09$; d.f. = 2, 115; $P < 0.0001$) instar larvae, but not in the third

Table 1. *Pre-imaginal development times and survival of three species of coccinellid reared on* Myzus persicae *at 25°C*

Species	*n*	X ± SE Developmental time (days)							Pre-imaginal survival X (%)
		Egg	Larva				Pupa	Total	
			First	Second	Third	Fourth	Total		
H. axyridis	42	2.8 ± 0.1 a	2.3 ± 0.1 a	1.5 ± 0.1 a	2.0 ± 0.1 a	4.7 ± 0.1 a	10.4 ± 0.2 a	6.6 ± 0.1 a	19.8 ± 0.2 a	49.4
H. variegata	53	2.6 ± 0.1 a	2.6 ± 0.1 b	1.9 ± 0.1 b	2.0 ± 0.1 a	2.9 ± 0.1 b	9.4 ± 0.2 b	6.1 ± 0.1 b	18.1 ± 0.3 b	49.1
A. bipunctata	25	2.3 ± 0.1 b	2.8 ± 0.1 b	1.6 ± 0.1 ab	1.8 ± 0.1 a	3.4 ± 0.2 b	9.6 ± 0.2 b	6.5 ± 0.1 a	18.4 ± 0.2 b	25.0

Mean values within a column followed by the same letter are not significantly different, $P < 0.05$, Tukey's (HSD) test.

($F = 1.07$; d.f. = 2, 115; $P = 0.3466$) (table 1). In particular the fourth instar larval development time of *H. axyridis* was 1.6 and 1.4 times longer than that of *H. variegata* and *A. bipunctata*, respectively. As fourth instar is characterized by a strong predatory activity and *H. axyridis* shows a strong intraguild predation (Hironori and Katsuhiro, 1997; Yasuda and Ohnuma, 1999; Yasuda et al., 2001) this factor may represent an advantage for the exotic. Moreover, the quicker development of first and second instar larvae, that are more prone to IGP attack (G. Burgio, unpublished data), may give *H. axyridis* a further advantage respect to native species. Pupal development time was shorter in *H. variegata* than in *H. axyridis* and *A. bipunctata* ($F = 6.58$; d.f. = 2, 115; $P = 0.002$). *Adalia bipunctata* showed the shortest embryonic development time ($F = 6.13$; d.f. = 2, 115; $P = 0.0029$).

The pre-imaginal development times of *H. axyridis* were found to be fairly much in line with those reported by other authors (Kim and Choi, 1985; Schanderl et al., 1985; Niijima et al., 1986; McClure, 1987; LaMana and Miller, 1998; Abdel-Salam and Abdel-Baky, 2001). In others studies *H. axyridis* took less time to complete its development (Baldacci, 1998; Phoofolo and Obrycki, 1998; Michaud, 2000). The development times reported by Michaud (2000) on *Aphis spiraecola* Patch were, instead, longer than that found in our experiment (table 2).

The pre-adult development times reported by Obrycki and Orr (1990) for *H. variegata* are quite close to ours, while those reported by ElHag and Zaitoon (1996) are slightly longer. According to El Habi et al. (2000) development from the first instar larvae to adult emergence took less time. The development times reported by Michels and Flanders (1992) for four strains of *H. variegata*, ranged from 23.9 to 30.0 days (table 2).

Our findings essentially agree with those reported by Obrycki and Tauber (1981) for *A. bipunctata*. Francis et al. (2001) found that the time taken by *A. bipunctata* to develop from egg to adult ranged from 21.8 to 23.4 days depending on host plant.

Significant differences were found in the survival percentage of the immature in the three species studied (table 1), the lowest pre-imaginal survival ($\bar{X} = 25.0\%$) being reported for *A. bipunctata*, compared with that of *H. axyridis* ($\bar{X} = 49.4\%$) ($\chi^2 = 11.85$; d.f. = 1; $P = 0.0006$) and that of *H. variegata* ($\bar{X} = 49.1\%$) ($\chi^2 = 18.12$; d.f. = 1; $P < 0.0001$). The low percentage of egg hatching (53% for *H. axyridis*, 73% for *H. variegata* and 55% for *A. bipunctata*) was the most significant factor accounting for the mortality observed by us throughout pre-imaginal development. Overall, the survival percentage findings of our study were lower than those reported by Kim and Choi (1985), Niijima et al. (1986), Schanderl et al. (1988), LaMana and Miller (1998), Phoofolo and Obrycki (1998), Michaud (2000) and Abdel-Salam and Abdel-Baky (2001) for *H. axyridis*, Obrycki and Orr (1990) and ElHag and Zaitoon (1996) for *H. variegata*, Obrycki and Tauber (1981) and Francis et al. (2001) for *A. bipunctata* (table 2). Kalushkov (1994), instead,

Table 2. *Summary of literature survey of pre-imaginal development times and survival values of three coccinellid species reared on different preys*

Coccinellid species	Prey	Host plant	Rearing temperature (°C)	Mean ± SD developmental time (days)	Pre-imaginal survival (%)	References
Harmonia axyridis	Fresh *Sitotroga cerealella* Oliver eggs	–	27	18.8 ± 0.32*	84	Abdel-Salam and Abdel-Baky (2001)
	Frozen *S. cerealella* eggs	–	27	22.5 ± 0.21*	80	
	Aphis gossypii Glover	*Cucurbita pepo* L.	25	14.9	96.7	Baldacci (1998)
	Frozen *Ephestia kuehniella* Zeller eggs	–	25	15.5	96.6	
	Acyrthosiphon pisum (Harris)	*Vicia faba.* L.	26	17.5 ± 1.1	88.7†	LaMana and Miller (1998)
	A. pisum	*V. faba*	27	18.6 ± 1.3	–	McClure (1987)
	Toxoptera citricida (Kirkaldy)	Carrizo citrange‡	23–24	15.3†	95.0	Michaud (2000)
	Aphis spiraecola Patch	*Viburnum odoratissimum* Kerr–Gawl	23–24	27.2†	70.0	
	Lachnus tropicalis (Van der Goot) powder	–		20.1 ± 0.3	84.0	Niijima et al. (1986)
	A. pisum powder	–		20.3 ± 1.1	80.0	
	Anuraphis nume powder	–		19.8 ± 0.4	88.0	
	Aphis rumicis (L.) powder	–		18.4 ± 2.88	80.0	
	A. pisum	–	26	14.6 ± 0.8†	–	Phoofolo and Obrycki (1998)
	Chrysoperla carnea Stephens eggs	–	26	14.0 ± 0.8†	–	
	M. persicae	–	25	18.6	–	Schanderl et al. (1985)
	A. gossypii Glover	–		19.92	85.9	Kim and Choi (1985)
Hippodamia variegata	*A. gossypii*	–	26	10.71 ± 0.69†	–	El Habi et al. (2000)
	Brevicoryne brassicae (L.) and *Rhopalosiphum padi* L.	Cabbage and wheat, respectively	25	20.1	61.8	El Hag and Zaitoon (1996)
	Rhopalosiphum maidis (Fitch)	*Hordeum vulgare* L.	23	19.4 ± 3.3*	95	Obrycki and Orr (1990)
	A. pisum	*V. faba*	23	19.3 ± 2.8*	88	
	Schizaphis graminum (Rondani)	–	20	30.3–24.4–26.1–24.8§	–	Michels and Flanders (1992)
	Diuraphis noxia (Mordvilko)	–	20	27.7–23.9–28.1–26.8§	–	
Adalia bipunctata	*M. persicae*	*Sinapis alba* L.	20	21.8 ± 0.8	85.0	Francis et al. (2001)
		Brassica napus L.	20	22.0 ± 0.7	86.7	
		V. faba	20	23.4 ± 1.0	87.8	
	A. pisum	–	24	17.8 ± 0.5*	70	Obrycki and Tauber (1981)

* Mean ± SE.
† First instar larvae to adult emergence.
‡ *Poncirus trifoliata* (L.) Osbeck X *Citrus sinensis* (L.) Rafinesque.
§ Four strains from Canada, Chile, Moldavia and Morocco, respectively.

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Table 3. *Reproduction parameters, longevity and sex ratio of three species of coccinellid reared on* Myzus persicae *at 25°C*

Species	*n*	Fecundity (no. eggs laid/ female)*	Oviposition rate (no. eggs laid/ female/day)*	Adult longevity (days)*	Pre-oviposition period (days)**	Oviposition period (days)**	Interoviposition period (days)*	Sex ratio (% females)
H. axyridis	15	560.5 ± 100.5 a	18.3 ± 2.5 a	27.5 ± 2.6 a	7.4 ± 0.3 a	13.7 ± 2.3 a	3.6 ± 0.8 a	39
H. variegata	20	841.7 ± 115.3 a	21.2 ± 1.9 a	36.9 ± 2.9 a	2.1 ± 0.2 b	32.2 ± 3.2 b	1.5 ± 0.4 b	52
A. bipunctata	20	537.0 ± 76.9 a	16.0 ± 1.9 a	30.7 ± 3.3 a	4.3 ± 0.3 c	24.7 ± 3.0 b	2.2 ± 0.4 ab	56

Mean values within a column followed by the same letter are not significantly different. * $P < 0.05$, ** $P < 0.01$, Tukey's (HSD) test.

has reported very high mortality rearing *A. bipunctata* on *Aphis fabae* Scopoli (83.3%) and on *A. fabae* plus *Aphis craccivora* Koch (90.0%). The methodology used to separate the eggs from their batches might have damaged some of them and this could explain the high embryonic mortality found in our experiments.

No significant differences in adult female longevity were found among the three coccinellid species ($F = 2.47$; d.f. = 2, 52; $P = 0.0945$) (table 3). A rapid decline in the survival curves was however observed after 30 days for *H. axyridis* and *A. bipunctata* (fig. 1). At 35 days the survivorship of these species was about 30%, whereas for *H. variegata* it was 60%. The highest adult longevity was 44 days for *H. axyridis*, 60 days for *H. variegata* and 61 days for *A. bipunctata* (fig. 1). Appreciably higher mean values of longevity have been reported by Hukusima and Kamei (1970) for *H. axyridis* on *M. persicae* and *Amphorophora oleracea* and by McClure (1987), Baldacci (1998) and Abdel-Salam and Abdel-Baky (2001). Higher values have also been reported for *H. variegata* by ElHag and Zaitoon (1996) and by Kalushkov (1994) for *A. bipunctata* on *Phorodon humuli* (Schrank). The latter author has however reported female adult longevity values similar to ours by feeding *A. bipunctata* on *A. fabae* and on *A. fabae* added with *A. craccivora* (Kaluskhov, 1998).

Differences were also observed in the mean pre-oviposition period of the three species examined ($F = 88.55$; d.f. = 2., 51; $P < 0.0001$) (table 3). The longest period was observed for *H. axyridis* (range 6–10 days), followed by *A. bipunctata* (range 3–8 days) and *H. variegata* (range 0–4 days). Frequency distributions of the pre-oviposition period are shown in fig. 2. Eighty per cent of the females of *H. axyridis* had a pre-oviposition period of 7–8 days, while the pre-oviposition period of 55% of *H. variegata* females and of 69% of *A. bipunctata* females ranged from 2 to 4 days. All females started to oviposit within 10 days of their adult life whereas delayed oviposition over 10 days was not observed for the three species studied. The mean interoviposition period was significantly higher in *H. axyridis* (range 0–10) compared with *H. variegata* (range 0–7) but not compared with *A. bipunctata* (range 0–6) ($F = 3.73$; d.f. = 2, 51; $P = 0.0309$). Frequency distribution showed that in the majority of females of *H. variegata* (90%) and of *A. bipunctata* (78%) the interoviposition periods ranged from 0 to 3 days (fig. 3), while only 53% of *H. axyridis* females had an interoviposition period of up to 3 days and 27% of 6 days.

Phoofolo and Obrycki (1995), studying four populations of *C. septempunctata*, reported that this ladybird exhibits a consistent bimodal pattern in the pre-oviposition and interoviposition periods: one group had short and another group had long (> 15 days) pre-oviposition and interoviposition periods. These authors concluded that the expression of a large range of variation in life-history traits related to fecundity, such as pre-oviposition and interoviposition periods, may be one of the factors responsible for the widespread occurrence of this ladybird in the United States. Our results show that in *H. axyridis*, neither pre-oviposition nor interoviposition frequency distribution exhibited the bimodal pattern reported

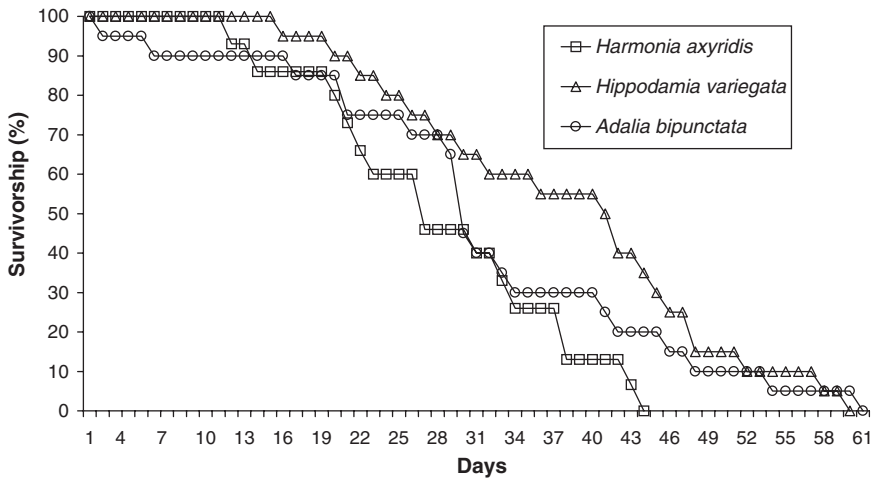

Fig. 1. *Female survival of three coccinellid species reared on* Myzus persicae *at 25°C*

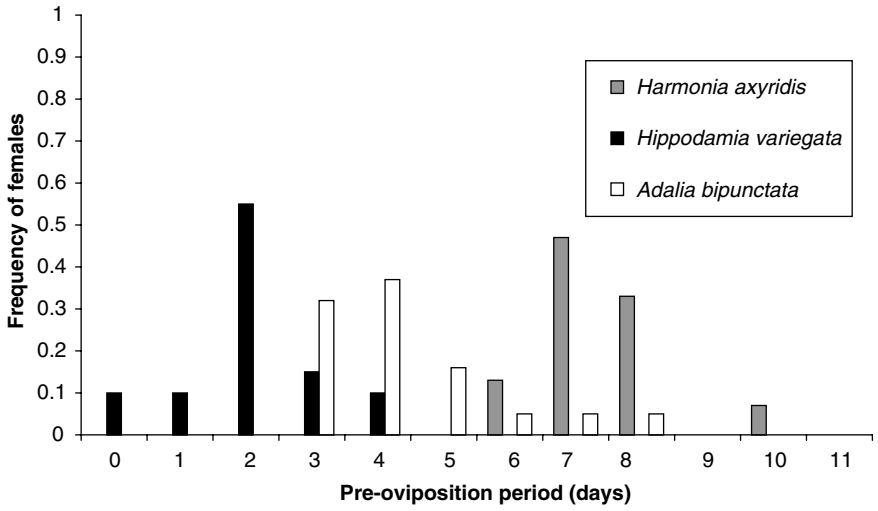

Fig. 2. *Frequency distribution of pre-oviposition period in three coccinellid species reared on* Myzus persicae *at 25°C*

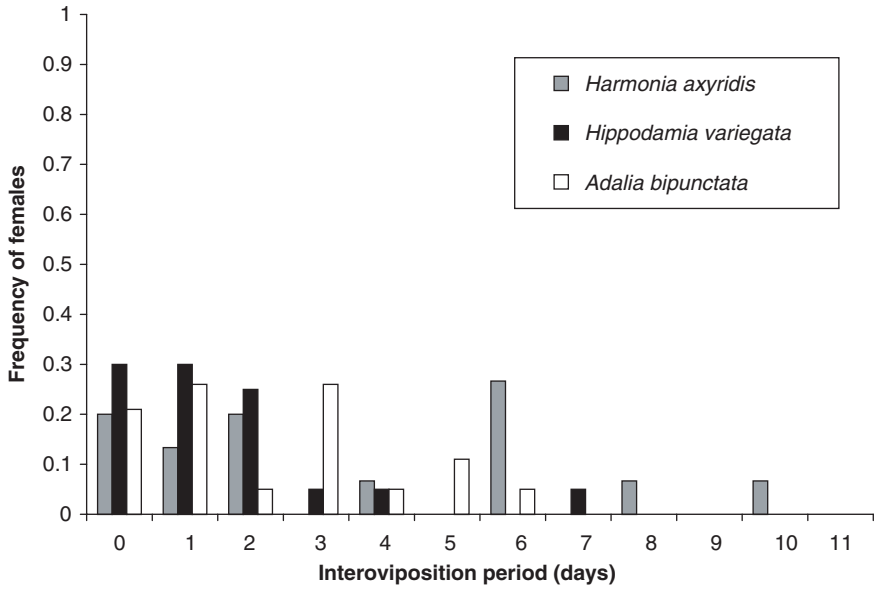

Fig. 3. *Frequency distribution of interoviposition period in three coccinellid species reared on* Myzus persicae *at 25°C*

by Phoofolo and Obrycki (1995) and by Hodek and Ruzicka (1979) for *C. septempunctata*. Lewontin (1965), studying the importance of age at first reproduction in the colonizing ability of organisms, underlines the influence of the pre-oviposition period on the variation of the intrinsic rate of increase. He concludes that species with low levels of variance in their age at first reproduction are characterized by having 'a long history of colonization'. It is because directional selection strongly effects the age at first reproduction during the colonization period. As expected following Lewontin's (1965) conclusions, the native species *H. variegata* and *A. bipunctata* showed a homogeneous pre-oviposition period. On the contrary, *H. axyridis* was expected to have a less homogeneous pre-oviposition period, because of its widespread occurrence in the United States. However, the biofactory strain used in our experiments may have undergone a selection towards a more homogeneous pre-oviposition period, during the rearing process. From these points of view, the biofactory strain of *H. axyridis* used in this study does not seem to have a high invasiveness capacity. The mean oviposition period of *H. axyridis* was significantly shorter than that of *H. variegata* and of *A. bipunctata* ($F = 9.26$; d.f. $= 2, 51$; $P = 0.0004$) (table 3). It was remarkably shorter also compared with the findings reported by Hukusima and Kamei (1970), by McClure (1987), and by Abdel-Salam and Abdel-Baky (2001) for the same species. The egg-laying period for *H. axyridis* ranged from 1 to 28 days, from 6 to 57 for *H. variegata* and from 2 to 50 for *A. bipunctata*.

The three species did not show any significant differences in fecundity or oviposition rates ($F = 3.06$; d.f. $= 2, 52$; $P = 0.0554$; and $F = 1.76$; d.f. $= 2, 52$; $P = 0.1818$, respectively), although the differences in fecundity were close to the 0.05 significance level (table 3). Despite the evidence that the longevity and oviposition periods found in our experiment are about three times less than those reported by McClure (1987) and by Abdel-Salam and Abdel-Baky (2001), the fecundity findings for *H. axyridis* are substantially in agreement with those observed by these authors. However, Baldacci (1998), who reported a higher longevity, also found a higher fecundity. The fecundity findings for *H. variegata* in our study are not

in line with those of ElHag and Zaitoon (1996), according to whom the average female produces 276.3 eggs at the rate of 10.6 eggs/day. Our fecundity findings for *A. bipunctata* were essentially in line with those of Hämäläinen et al. (1975). A higher fecundity on *P. humuli* has instead been reported by Kalushkov (1994), which was found to be much lower when the ladybeetle was fed on *A. fabae* and on *A. fabae* together with *A. craccivora*.

The curves of Bieri model, that fits the age-specific fecundity, for the three species of coccinellids, are shown in fig. 4. The highest daily mean oviposition value was recorded at 16 days for *H. axyridis*, at 24 days for *H. variegata*, and at 22 days for *A. bipunctata*. A similar peak value was found by Kariluoto (1980) for *A. bipunctata* reared on *M. persicae*.

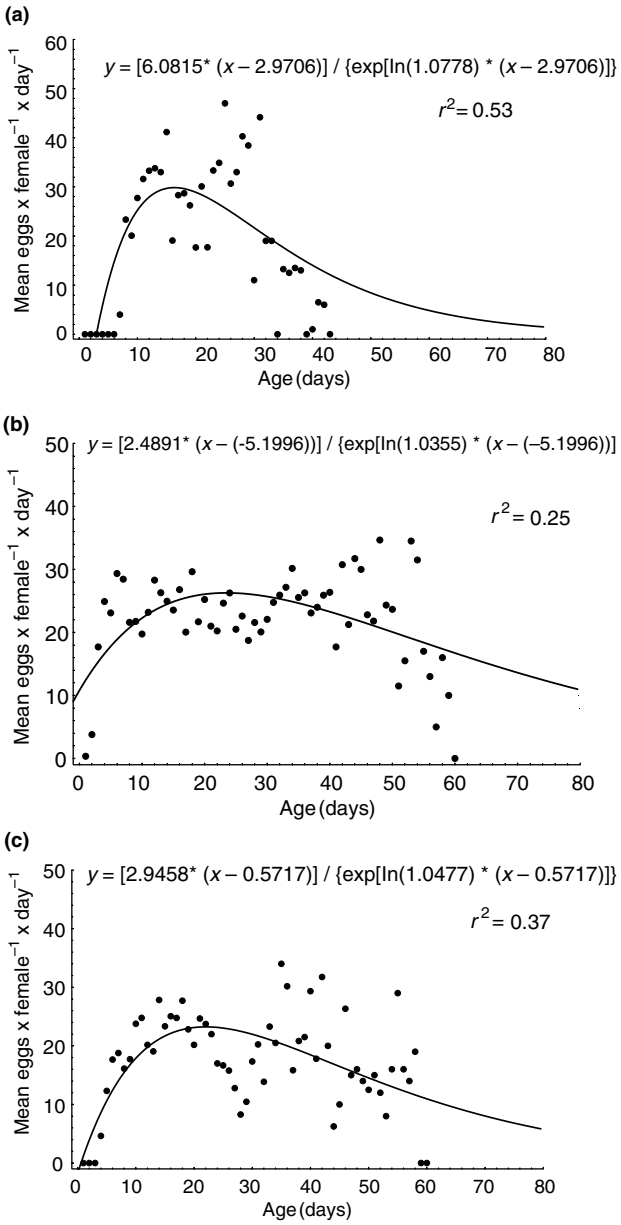

Fig. 4. *Oviposition rate as a function of age (days) (Bieri model) of* Harmonia axyridis *(a),* Hippodamia variegata *(b) and* Adalia bipunctata *(c) reared on* Myzus persicae *at 25°C*

A comparison of our findings with those of other studies (e.g. Kalushkov, 1994 for *A. bipunctata* and Snyder et al., 2000 for *H. axyridis*) confirms that factors such as prey species, cannibalistic feeding, and rearing conditions, that may affect development duration, mortality and adult longevity in coccinellids, are of considerable importance. Moreover, as suggested by Francis et al. (2000, 2001) for *A. bipunctata* and Giles et al. (2002) for *C. septempunctata*, it is important that the biological traits of coccinellids be considered in a tritrophic contest. In fact, according to Kalushkov (1998), who analysed development time, mortality and adult weight, the suitability of *A. fabae* as food for *A. bipunctata* depends on its host plant. Moreover, survival, developmental time and size of *C. septempunctata* appear to be modulated by the biochemical response of the aphid prey to host plant (Giles et al., 2002). As suggested by Francis et al. (2000, 2001), host plant allelochemical substances may not only affect the herbivores but also the pest predators.

The intrinsic rate of population increase, net reproductive rate and mean generation time are given in table 4. Compared with the other species studied, the highest values for all parameters were recorded for the native *H. variegata*, and the lowest for *A. bipunctata* except for *T* where *H. axyridis* showed the lowest one. In particular, the net reproductive rate of *H. variegata* was 1.5 and 2.9 times higher than that of *H. axyridis* and *A. bipunctata*, respectively. Our findings showed that the potential for population increase of the exotic species *H. axyridis* is slightly greater than that of *A. bipunctata* but lower than that of *H. variegata*. Such a finding is probably ascribable chiefly to the higher development time from egg to adult of *H. axyridis* and to the low pre-imaginal survival of *A. bipunctata*. A comparison between the life table parameters of *H. axyridis* and those of other native ladybirds shows that the potential for population increase is greater also for *Propylea quatuordecimpunctata* L. ($T =$ 33.0 days, $R_0 = 149.9$, $r_m = 0.15$) (Obrycki et al., 1993) and *C. septempunctata* ($T = 34.0$ days, $R_0 =$ 567.6, $r_m = 0.19$) (Phoofolo and Obrycki, 1995).

In conclusion, while *H. axyridis* is indeed an easy-to-rear and good predator for the control of aphid outbreaks, our study shows that under laboratory conditions and using *M. persicae* as prey, it does not exhibit a higher capacity for population increase when compared with that of other native coccinellids. How-

Table 4. *Estimated laboratory life-table parameters for three species of coccinellid reared on* Myzus persicae *at 25°C*

Species	Life table parameters		
	T	R_0	r_m
H. axyridis	38.81	26.27	0.089
H. variegata	41.88	52.75	0.114
A. bipunctata	40.06	18.49	0.081

ever, to evaluate the environmental risk of the introduction of exotic natural enemy used in inundative biological control, especially for highly polyphagous predators like *H. axyridis*, life-table data must be integrated by other information such as its capacity to establish, its abilities to disperse, its host range, and direct and indirect effects on non-targets (van Lenteren et al., 2003). Moreover, life history data are of basic importance in an effort to develop a modelistic approach to study interspecific interaction among exotic and native species. Although our present findings show that the biological traits of *H. axyridis* are not factors that may contribute to the invasiveness of this coccinellid, van Lenteren et al. (2003) found the highest risk indexes for generalist predatory insects including *H. axyridis*. Moreover, many authors (see Introduction) have highlighted the impact of the introduction of *H. axyridis* in the United States. This scenario could depend on other reasons, including intra-guild predation (Phoofolo and Obrycki, 1998; Burgio et al., 2002; Santi et al., 2003) in particular of the fourth instar larvae (G. Burgio, unpublished data), overwintering capacity (Cartwright et al., 1982; Bazzocchi et al., 2004) and also different impact of shared coccinellid parasitoids (Cartwright et al., 1982; Obrycki, 1989) and pathogens (Cartwright et al., 1982).

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Author's address: Giovanni Burgio (corresponding author), Dipartimento di Scienze e Tecnologie Agroambientali-Entomologia, Alma Mater Studiorum-Università di Bologna, viale G. Fanin 42, I-40127 Bologna, Italy, e-mail: gburgio@entom.agrsci.unibo.it